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THE COLONY FOUNDING OF *ACANTHOMYOPS*
(DENDROLASIUS) FULIGINOSUS LATR.

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PUTNEY, ENGLAND.

Mons. R. Stumper ('20), having recently recorded the discovery of three isolated *fuliginosus* females in cells under stones, considers that these facts alone diminish the probability that the manner of starting colonies adopted by the *fuliginosus* is the dependent one, and that further investigation may prove this. We are personally of the opinion that the colony-founding habits of this ant are now well known and thoroughly established, not only by discoveries in the field, but by exhaustive experiments carried out in the laboratory. We propose to review the entire evidence on the subject in the order of date on which the various records and discoveries have been made; and to deal, therefore, with Mons. Stumper's remarks at the end of the paper.

Donisthorpe ('97) records that he found at Lymington a large colony of *A. (D.) fuliginosus* nesting in a hollow tree, and that a colony of *A. (Chthonolasius) flavus* was living in the same nest, both species coming in and going out together. With our present knowledge we know that it would be impossible for *fuliginosus* and *flavus* to live together, and that instead of the latter ant the species must have been *umbratus* or *mixtus*.

De Lannoy ('08) writes that in 1904 he found at Knoche-sur-Mèr in Belgium a few workers of *mixtus* living in a large colony of *fuliginosus*, and in 1906 he again found several similar colonies. He suggested as an explanation that the *fuliginosus* had stolen the larvæ and pupæ from a colony of *mixtus* which they had attacked, and that a few of the latter's brood, which had not been devoured, had been reared in the nest of the former ant.

Forel ('08) and Emery ('08), when commenting on de Lannoy's suggestion, expressed the view that it was a case similar to those in the *Formica* groups where the females have lost the power of founding their colonies unaided, and that a female *fuliginosus*

after the marriage flight had been accepted into a nest of *mixtus*. After the natural or violent death of the *mixtus* queen, the brood of the *fuliginosus* queen had been brought up by the *mixtus* workers; the black ants gradually increasing and the yellow dying off little by little, until eventually a pure black colony was left.

Wasmann ('09) called attention to the ability of *fuliginosus* to form new colonies by sending off detachments of queens and workers after the manner of *Formica rufa*. He further accepted the interpretation given by Forel and Emery of de Lannoy's discoveries, and recalled the fact that he had himself on several occasions found mixed colonies of *fuliginosus* and *umbratus*. He hoped that future experiment would clear the matter up.

Crawley ('10) records that in 1898 he frequently found workers of a large bright yellow ant among the workers of a *fuliginosus* colony nesting in his house near Oxford. He thought at the time that the yellow individuals were workers of *flavus*, but is now satisfied that they were *umbratus*.

Donisthorpe ('10) points out that colonies of *fuliginosus* are often numerous in a district in which it occurs, and that it partly founds its colonies by branch nests. He mentions that Wasmann had frequently found *umbratus* nests at the foot of trees inhabited by *fuliginosus*, and that the queen of the latter had probably founded her colony in the nest of the former. He refers to Crawley's record of *umbratus* workers in a *fuliginosus* nest and to his own of 1897. He says he is now convinced that the species was really *umbratus*; he was not so well acquainted with our ants at the time, but he remembers distinctly thinking how large the "flavus" were.

Wheeler ('10), when describing an aberrant *Lasius* from Japan, discusses thoroughly the colony founding of *fuliginosus*. He writes: "Unlike the queens of the common *Lasius niger*, the queen of *fuliginosus*, after fecundation on her marriage flight, and on returning to the earth, is unable to start a colony unaided, and if prevented from rejoining the maternal colony, or a detachment of workers of her own species, has to seek out a colony of *L. umbratus* and have her young brought up by the workers of this ant. The *umbratus* queen must be killed either by her own workers or by the intrusive *fuliginosus* queen, so that the host species is destined

eventually to die off and leave a pure and thriving *fuliginosus* colony." That this method of colony founding is actually adopted by *fuliginosus* queens is clearly indicated by the following observations which have been slowly accumulating during the past few years. He then proceeds to review the writings of Crawley, Donisthorpe, Emery, Forel, de Lannoy, and Wasmann; and gives some further illuminating and interesting remarks on the genus *Acanthomyops (Lasius)*.

Donisthorpe ('11a), in a paper read before the Entomological Society of London on December 7, 1910, mentions briefly all that was known to date on the colony founding of *fuliginosus*, referring to the writings and views of all the above-mentioned myrmecologists. He further says that a worker of *umbratus* had been sent to him to name on September 20, 1900, by a Mr. Tuck, who had taken it in a *fuliginosus* nest situated in a horse-chestnut stump at Bury St. Edmunds. He then stated: "My friend Mr. Crawley and I intend to carry out experiments with *fuliginosus* queens and observation nests of *umbratus* next year."

Donisthorpe and Crawley ('11b), in a paper read before the Entomological Society of London on November 15, gave the results of the above-promised experiments, which they published in detail. These experiments were entirely successful, and proved without doubt that a female *fuliginosus* will be accepted and her brood be brought up by the *umbratus* workers. They reviewed all the previous discoveries and gave a complete list of the literature on the subject.

The same two authors ('13), in a voluminous paper on the founding of colonies by queen ants read at the Second International Congress of Entomology held at Oxford in 1912, gave a very complete account of the colony founding of this ant, including all experiments and discoveries, in detail, made up to date.

Donisthorpe ('13), in a paper on some remarkable associations between ants of different species read before the Lancashire and Cheshire Entomological Society, briefly referred to the colony founding of *fuliginosus* queens in nests of *umbratus* and *mixtus*.

Donisthorpe ('15a), in his book on "British Ants," gives a full account of the colony founding of this species. It seems as well to reproduce the whole of this account here, as it gives the main

facts of the experiments by Crawley and himself referred to above (which would have taken up too much space to give in detail in this paper), and records further experiments. "Crawley and I have shown that the female (*fuliginosus*) does not lay till the year after impregnation, and we have proved her to be a temporary social parasite, as will shortly be seen. . . . *D. fuliginosa* often founds new colonies by branch nests, which accounts for the fact that many colonies are found in the districts where this ant occurs. After the marriage flight newly fertilized females are received back into the parent and other *fuliginosa* nests near by. Occasionally, however, deälated females are found wandering about in localities some distance from their nests. Forel records finding a number of deälated females on roads at Soleure on July 21, 1869, and Crawley found one at Oddington, near Oxford, about one hundred yards from a nest, and others at Esher in August, 1899, and in such cases as these the females would not be likely to be received back into their own nests. However, when isolated they display no desire to found a colony. Crawley and I have both kept in captivity newly fertilized females which get rid of their wings immediately after impregnation; and they never settle down, but endeavor to escape, and soon perish.

"Therefore, from the above facts alone, it seems doubtful whether the female of this species can found a colony unaided. But further observations in the field point to *umbratus* and *mixtus* as the host species of *fuliginosus*. In 1897 I found at Lymington a large colony of *fuliginosus* in a hollow tree, and *umbratus* was undoubtedly living with it, as workers of both species were going in and out of the same holes. Crawley in 1898 repeatedly found workers of *umbratus* walking unmolested with the workers of a large nest of *fuliginosus* established under his house near Oxford. In September, 1900, Tuck sent to me a worker of *umbratus* taken in a nest of *fuliginosus* at Bury St. Edmunds. In 1904 de Lannoy found at Knoche-sur-Mèr a few workers of *mixtus* in the midst of a large colony of *fuliginosus* which were on good terms with the workers of the latter, and in 1906 he again found workers of *mixtus* in several *fuliginosus* nests. Forel, Emery, Wasmann, Wheeler, and I commented on de Lannoy's observations, and expressed the opinion that the presence of these *mixtus* workers was

due to the fact that fertile *fuliginosus* females had entered nests of the former species and been accepted. The queens of the *mixtus* had then died, or had been killed, either by their own workers or by the *fuliginosus* females, and the offspring of the latter were reared by the *mixtus* workers. In the course of time many of the latter had died off, and the few found in the nests were the survivors of the original *mixtus* colonies.

"Crawley and I determined to test this hypothesis by experiments on captive colonies. In July, 1910, a portion of a nest of *fuliginosus* was dug up at Darenth Wood, containing a quantity of workers, larvæ, males, and winged females, but no queen. The ants and brood were divided into two equal portions and each established in a four-chambered 'Janet' nest. (It may be here mentioned that this ant can not be kept in close confinement, but that if an observation nest be connected by long glass or india-rubber tubes to another plaster nest, or glass bowl, or some other contrivance in which their food is placed, the ants will thus obtain sufficient exercise.) During July all the males died and most of the females, with the exception of about twelve, which were found to be deälated. As some of these latter subsequently laid eggs, from which larvæ were reared, it is highly probable that mating had taken place inside the nests.

"In the beginning of December, 1910, a nest of *umbratus* without a queen was obtained at Weybridge and divided into two equal portions, which were established in 'Janet' nests. The first experiment was made on December 10, when one of the deälated female *fuliginosus* was placed in the light chamber of one of the *umbratus* nests. She immediately entered the most crowded chamber; one worker saluted her and another dragged her further by a mandible, but eventually she was attacked and killed before evening. On December 13 another deälated female was put into a small plaster nest with some of the workers from the same *umbratus* nest as in the former experiment. She was slightly attacked, but made no resistance, and endeavored to conciliate her assailants by stroking them with her antennæ. When a worker endeavors to bite at the waist of one of these females, she protects it by crossing her hind legs over her back, and when at the neck by pressing her head back close against the thorax. A few more workers were added,

and on December 20 she was introduced with the workers into the *umbratus* nest. She was a little attacked by workers who had not seen her before, but the old workers protected her, getting between her and the others, and pulling them away by the leg, but very soon all hostility ceased, and she was evidently accepted. Many workers surrounded her, caressed and fed her, and all went well till April, when, a number of the workers having died off, some four hundred more were obtained from the Weybridge nest and introduced. These newcomers attacked the queen, though they were quite friendly with their sister workers, and as they persistently refused to accept her, she was removed and returned to her own nest on April 21. The *fuliginosus* workers were very excited at her appearance in their nest, and she was much pulled about, but eventually lost sight of amongst the crowds of ants. On July 23 a female with her gaster enormously dilated was noticed in the *fuliginosus* nest, with a large pile of eggs and surrounded by workers, which may possibly have been the female of the above experiment. In the next experiment a female *fuliginosus* was still more easily received into the other *umbratus* nest, and by December 16 she was completely accepted. On March 22, 1911, another *fuliginosus* was introduced into this nest and was immediately accepted without any hostility whatever, as was the case with two more which were introduced in April, but subsequently removed. The two queens first introduced in this experiment began to lay on March 17, 1911, for the first time, and these eggs hatched on August 9. In 1912 they began to lay on June 29, and laid more eggs than during the previous year, but nothing came of these. Some of the larvae which hatched in August, 1911, were nearly full grown in the summer of 1912, but they remained in this condition until 1914. A larva first pupated on June 23, 1914, and several more subsequently, but none of them reached the perfect state. As these were from eggs laid in May, 1911, it will be seen that they took over three years to develop as far as the pupal stage!

"In 1913 I made a similar experiment with a nest of *mixto-umbratus* obtained at Weybridge on August 11, 1912, and subsequently strengthened with workers of *umbratus* from Wellington College. On September 14, 1913, two fertilized females, from the Oxshott nest before mentioned which had just removed their

wings, were introduced into the *mixto-umbratus* nest, when they were very little attacked and completely accepted the same day. The one died on October 12, but the other has been treated by the workers as their queen, having been fed, cleaned, and caressed by them, and is still alive in this nest—she laid her first eggs on July 12, 1914. As the females of *fuliginosus* are only slightly larger than the workers, and as their fertility is delayed for so long a period, it is clear that they are unable to found colonies unaided; they are hyper-temporary social parasites, since, as will be seen presently, *umbratus* and *mixtus* are temporary social parasites of *niger* and *alienus*."

Donisthorpe ('15b) recorded the death on August 29, 1915, of the above-mentioned *fuliginosus* queen which had been accepted on August 11, 1912, into a colony of *mixto-umbratus*. The workers in this nest had all gradually died off, and a large number of fresh *umbratus* workers were obtained from Woking and put into the nest. These accepted the old *fuliginosus* female at once. She was very weak and died a few days afterwards, but not from injuries. The workers had never shown any animosity toward her, treating her from the first as their queen.

Donisthorpe ('16), having been left with the above-mentioned queenless *umbratus* nest, obtained a number of virgin *fuliginosus* females from a colony of that ant nesting in the ground under a broom bush at Weybridge. On September 3, 1915, he removed the wings from one of these females and introduced her into the observation nest containing the *umbratus* workers. She ran about among the *umbratus* workers, tapping them with her antennæ; she was not attacked and soon gained the last (dark, damp) chamber of the nest, which contained the bulk of the *umbratus*. She appeared to have been accepted at once and was saluted, cleaned, and fed by some of the workers. She was treated as their queen, and was not attacked until September 7, when, the nest having been left in the sun, some of the workers began to attack her and pull her about. The nest was placed in a cool, dark place, and by September 19 she was once more thoroughly accepted as queen; she has not been attacked since, and on December 19 she was surrounded by a large court of attendant ants. Wheeler first demonstrated that if the wings be removed from a virgin *Formica* female

it causes her to behave as would a fertilized one. I have subsequently found this to be the case in all such experiments with *Formica* females. In the genus *Acanthomyops*, Crawley has recorded that the act of removing the wings from virgin *umbratus* females was far from arousing the instincts possessed by a fertilized queen. In the above-mentioned experiment with a virgin female of *fuliginosus*, however, the effect caused by removing the wings was to make her act undoubtedly as would a fertilized queen.

Donisthorpe ('17) continues the story of the virgin *fuliginosus* female mentioned above. By April 22, 1916, her gaster had commenced to swell, and on May 25 she laid a few eggs. On June 9 a larger packet of eggs was present, held up in one mass by several of the *umbratus* workers. On June 25 two larvæ had hatched, the eggs having taken over two months to develop. The eggs continued to hatch very slowly, and on November 28 some fifteen small larvæ were present. On January 28, 1917, ten medium-sized larvæ were counted, and the *fuliginosus* female was surrounded by a number of the *umbratus* workers.

Donisthorpe ('18) reports further concerning this *fuliginosus* female. On May 1, 1917, a fresh packet of eggs had been laid and the gaster of the female was considerably swollen. On May 22 there were present over 200 *umbratus* workers, the *fuliginosus* female, one packet of eggs, and 9 full-grown larvæ. May 24 some of the *umbratus* workers were covering the larvæ with bits of plaster, etc., to help them to spin their cocoons. Unfortunately during the author's absence in June and July the nest was allowed to get too dry, and on his return he found the eggs, larvæ, and pupæ had disappeared, and most of the *umbratus* workers had died. On August 18 a number of *Acanthomyops* (*Donisthorpea*) *niger* worker cocoons from Woking were introduced, and these were collected by the few remaining *umbratus* workers. The workers from the *niger* cocoons began to appear on August 26, and by October 13 all had emerged and were surrounding the *fuliginosus* queen. A number of fresh *umbratus* workers were brought home from Weybridge on October 16 and a few at a time were introduced into the nest to strengthen the colony. At first the *niger* workers killed them, and this went on till November, when a few were received. From then onwards four, five, and six *um-*

bratus workers were added every day, the *niger* workers no longer attacking them; neither did they attack the *niger* workers, nor the *fuliginosus* queen. The latter began to swell with eggs again on November 20. On December 31, 1917, there were present 60 *niger* workers and a large number of *umbratus* workers; the latter now surrounding the *fuliginosus* queen.

Donisthorpe ('19) mentions that in 1918 the *umbratus* workers in the above-mentioned nest started to kill the *niger* workers, all having been killed by May 17, 1918, when only one remained, which was killed before the end of the month. The *fuliginosus* queen gradually got very swollen again, and by May 27 she had laid a small bunch of eggs, which was held up by several *umbratus* workers. On June 16 two packets of eggs were present, but they were all eventually devoured by the *umbratus* workers. (The following is extracted from my notebook and has not been published before. The virgin female *fuliginosus* died in May, 1919, having lived in captivity for nearly four years. On April 25, 1919, she was very swollen with eggs, but almost dead, being held up by a number of the *umbratus* workers; and on May 1 she was quite dead, but still carried about by the workers until May 17, when her body was cut up. The *umbratus* workers then commenced to die off, so they were turned loose in the garden in June.) He further records that on July 17, 1918, he discovered in the New Forest a very interesting mixed colony of *A. (D.) fuliginosus* and *A. (C.) mixtus*, which consisted of about two thirds of the former workers to one third of the latter. The two species were walking along together in files on a fence near a railway bridge; they were quite friendly, tapping antennæ and saluting each other when they met on the tracks, as also when placed together in a small tube. The tracks led right down the brickwork of the bridge to the ground beside the line. It was really a beautiful sight, when the sun was shining, to see the jet black *fuliginosus* and yellow *mixtus* marching in files up and down the wall of the bridge and saluting each other when they met. As *mixtus* is very subterranean in its habits, it must have learned from the *fuliginosus* to march in files in the open. The tracks also led to and from a thick bramble grove growing by the side of a fence along the buttress of the bridge, and here the nest was evidently situated. He pointed out

that here was a case where a *fuliginosus* female had evidently founded her colony in a nest of *mixtus*.

On May 29, 1919, Mr. H. M. Hallett discovered a mixed colony of *fuliginosus* and *mixtus* in a wood at Cwrt-yr-ala in Glamorganshire. The shoots from the stump of a felled oak were covered with Aphides, and all over the stump and shoots numbers of *fuliginosus* and *mixtus* workers occurred together. They were in the proportion of about 6 to 4.

Stumper ('20) briefly refers to de Lannoy's records and the views held on the subject by Emery, Forel, and Wasmann. He considers that three, in particular two, discoveries he made in the summer of 1917 at Neuenstadt speak against the general validity of their opinions. There he found two isolated *fuliginosus* queens "in their cells," situated under stones; but no brood was present. The third was under a stone which covered a nest of *mixtus*, but "her cell" did not communicate with the galleries of the latter. It will be seen that his knowledge of the literature on the subject does not appear to extend beyond 1909—at any rate, he entirely ignores everything that has been written by Crawley, Donisthorpe, and Wheeler! His latest discovery, of course, really confirms the fact that *fuliginosus* females found their colonies in *mixtus* nests. The female in question was no doubt only waiting for a suitable opportunity to enter the *mixtus* nest. She was probably "in quarantine," for the same reason that beetles of the genus *Atemeles* hang about a nest of *Formica* before they enter it after leaving one of *Myrmica*. It is only in observation nests that a *fuliginosus* queen has to put up with such a severe test as going straight into a nest of the host species from her own. After fertilization, should a female not be able to return to the parent colony, or enter a nest of another colony of the same species, she would have to wander about in search of a *mixtus* or *umbratus* nest, and would naturally hang about near by after she had discovered it. She would not only thus lose her own nest "aura," but in part acquire that of the other. As to Stumper's two first instances, it is possible that there may have been colonies of *umbratus* or *mixtus* in the near vicinity. Or after hunting about in vain for such these females may have crept under stones for shelter. It is not to be supposed that every female who finds herself stranded is successful in her

search for colonies of her hosts. Finally, as we have already shown, *fuliginosus* females are not much larger than their workers, and do not possess large gasters supplied with plenty of fat to enable them to bring up their brood unaided, especially taking into consideration their long-delayed fertility. *Moreover, it has also been proved by experiment that they are unable to do so!*

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